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Fractal analysis of canopy architectures of *Acacia angustissima, Gliricidia sepium*, and *Leucaena collinsii* for estimation of aboveground biomass in a short rotation forest in eastern Zambia

Martin. L. Kaonga

Abstract: A study was conducted at Msekera Regional Agricultural Research Station in eastern Zambia to (1) describe canopy branching properties of *Acacia angustissima, Gliricidia sepium* and *Leucaena collinsii* in short rotation forests, (2) test the existence of self similarity from repeated iteration of a structural unit in tree canopies, (3) examined intra-specific relationships between functional branching characteristics, and (4) determine whether allometric equations for relating aboveground tree biomass to fractal properties could accurately predict aboveground biomass. Measurements of basal diameter (D_{10}) at 10cm aboveground and total height (H), and aboveground biomass of 27 trees were taken, but only nine trees representative of variability of the stand and the three species were processed for functional branching analyses (FBA) of the shoot systems. For each species, fractal properties of three trees, including fractal dimension (D_{fract}), bifurcation ratios (p) and proportionality ratios (q) of branching points were assessed. The slope of the linear regression of p on proximal diameter was not significantly different (P < 0.01) from zero and hence the assumption that p is independent of scale, a pre-requisite for use of fractal branching rules to describe a fractal tree canopy, was fulfilled at branching orders with link diameters >1.5 cm. The proportionality ration q for branching patterns of all tree species was constant at all scales. The proportion of q values >0.9 (f_q) was 0.8 for all species. Mean fractal dimension (D_{fract}) values (1.5−1.7) for all species showed that branching patterns had an increasing magnitude of intricacy. Since D_{fract} values were ≥1.5, branching patterns within species were self similar. Basal diameter (D_{10}), proximal diameter and D_{fract} described most of variations in aboveground biomass, suggesting that allometric equations for relating aboveground tree biomass to fractal properties could accurately predict aboveground biomass. Thus, assessed *Acacia, Gliricidia* and *Leucaena* trees were fractals and their branching properties could be used to describe variability in size and aboveground biomass.

Introduction

Recognition of the potential role of short rotation forests in terrestrial carbon (C) sequestration has, in the recent past, heightened interest in measuring and monitoring C stocks in agroforestry (Lott et al. 2000; IPCC 2006, 2007; Kaonga and Coleman 2008). Biomass estimates are useful for quantifying net primary productivity, nutrient and C cycles, and harvestable biomass yields, and for evaluating habitats and combustible fuel in these systems, (Saint-André et al. 2005; Delitti et al. 2006; Sağlan et al. 2008). However, periodic measurements and verification of plant C stocks in forest ecosystems requires use of cost-effective and reliable methods (IPCC 2006). Aboveground tree biomass can be measured directly by felling the tree, oven drying, and then weighing all botanical components (IPCC 2006; Kaonga and Bayliss-Smith 2009). However, this technique is laborious and time-consuming, and cannot be applied in long-term carbon forestry activities, in which destructive sampling is not feasible. Therefore, non-destructive techniques for estimation of tree biomass have been developed for forests (Brown et al. 2004; Kale et al. 2004; Delitti et al. 2006) and agroforestry systems (Jackson et al. 1995; Ong et al. 2004).

Allometric equations ($Y = a\ D^b$) based on height (H) and diameter at breast height (DBH) are often used to assess biomass and C stocks in forests (Brown 1997; Van et al. 2000; Claesson et al. 2001; Saatchi et al. 2007) and agroforestry systems (Jackson et al. 1995; Otieno et al. 1991; Kumar and Tewari 1999; Lott et al. 2000; Kaonga and Bayliss-Smith 2010). However, their scaling rules need re-calibration for each tree species and stand density, and cannot be easily applied in spatially-mixed agroforestry systems or in land-use systems where trees grow in more

Martin. L. Kaonga
A Rocha International, Sheraton House, Castle Park, Cambridge CB3 0AX, United Kingdom. E-mail: kaongamartin@hotmail.com;

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open conditions rather than in a closed stand (Brown et al. 1995; Kettering et al. 2001). The use of allometric equations in agroforestry systems is complex because (1) these equations are influenced by intensive management of system components (Cannell 1983), (2) as the tree approaches maturity, a very high percentage of aboveground biomass may not be accounted for by measurement of main stem allometrics, especially in multi-stemmed species (Jackson et al. 1995), (3) within the lifecycle of a tree, plant growth changes from linear to a non-linear pattern (Jackson et al. 1995), and (4) it is difficult to judge how well the biomass functions would perform with either other varieties or with same species grown in geographically matched locations (Lott et al. 2000). In such situations, fractal models could be used to predict aboveground tree biomass (Lott et al. 2000; Smith 2001; Van Noordiwjk and Mulia 2002).

The fractal theory is based on the existence, within an object, of self similarity arising from repeated iteration of a structural unit which forms a nested replica of the object at multiple scales and the same rules govern branching at each subsequent level (van Noordiwjk and Mulia 2002; Richardson and zu Dohna 2003; Koziowski et al. 2004; Brown et al. 2005; Price and Enquist 2007; Allen et al. 2008). In plants, canopy branching has a fractal pattern if the rules governing branching are independent of scale (Gisiger 2001; Camarero et al. 2003; Halley et al. 2004; Brown et al. 2005; Makela and Valentine 2006). The fundamental physical and biological principles as well as features of architecture, biomechanics, and hydrodynamics of vascular plants determine branching pattern in trees (West et al. 1999; Enquist 2002). To ensure optimal transportation of resources, mechanical stability, and resource use efficiency, a tree comprises discrete tree-like constructional units from the trunk to the smallest distal branches and structure (Bertram 1989). Therefore, fractal analysis of an individual tree will minimize variability since all units share a common genotype and growth environment, thus providing an opportunity to distinguish between even subtle differences in scaling.

Fractal properties of trees have been used to estimate root lengths (Nygren et al. 1998; Smith 2001), root size (Spek and van Noordwijk 1994; Van Noordwijk et al. 1994; Ozier-Lafontaine et al. 1999), root mass (Ozier-Lafontaine et al. 1999), root architecture (Fitter and Stickland 1992; Masi and Maranville 1998; Ozier-Lafontaine et al. 1999), and aboveground tree morphometry (McMahon and Kronauer 1976; Bertram 1989; Niklas 1995; van Noordwijk and Mulia 2002). Fractal properties of the tree canopy can also be used to predict aboveground biomass (Van Noordwijk and Mulia 2002). For example, diameter measurements of all branches were used to estimate biomass of *Grevillea robusta* in Kenya (Lott et al. 2000). Although fractal branch modelling has been used to predict root architecture and other properties, there is limited evidence on its application in aboveground biomass estimation.

This study tested the hypothesis that if the shoot system has a fractal structure, measured fractal properties could be used to estimate aboveground tree biomass in improved fallows. It specifically (1) described canopy branching properties of *Acacia angustissima*, *Gliricidia sepium* and *Leucaena collinsii* using

fractal analysis, (2) tested the existence of self similarity from repeated iteration of a structural unit in tree canopies, (3) examined intra-specific relationships between functional branching characteristics of canopy architectures, and (4) determined whether allometric equations for relating aboveground tree biomass to stem diameter can be predicted from fractal properties. The models will be used to measure, monitor, and verify aboveground tree biomass and C stocks in C forestry projects for C trading and screening of tree species.

Methodology

The fractal model

Fractal analysis of canopy architectures of three tree species at Msekera was based on assumptions described by Spek and van Noordwijk (1994) and Van Noordwijk et al. (1994):

(1) The topologies of shoot systems of *Acacia*, *Gliricidia*, and *Leucaena* species were described as networks made up of connected links with length and diameter measurements that are branch order independent.

(2) The shoot system is designed based on a recursive algorithm that is applied until the final branch of the network or minimum link diameter (D_{min}) is reached.

(3) The distribution of the number of daughter links (n) at any branching point follows a uniform law ($n \geq 2$).

(4) The sum of squared diameters of the new links is estimated from the previous link and the bifurcation ratio (p) parameter is assumed to be invariant whatever the branching event:

$$p = D_i^{\,2} / \sum_j^n D_{i+1,j^2} \qquad (1)$$

describes the change in diameter (D) from link order i (parent) to its n derivative links of order $i+1$ (daughter). Relative equity (q) that describes relative equity among branches at each branching event is expressed as:

$$q = D_{i+1,1^2} / (D_{i+1,1^2} + D_{i+1,2^2}) \qquad (2)$$

for n = 2 and $D_{i+1,1^2} > D_{i+1,2^2}$ $(0.5 < q \leq 1)$

At any given branching point generating n new links, the diameter of the thickest daughter link (D_l) is calculated as follows:

$$D_{i+1,1} = D_i (q/p)^{\frac{1}{2}} \qquad (3)$$

$$D_{i+1,2} = D_i (1-q/p)^{\frac{1}{2}} \qquad (4)$$

The fractal model will hold only if parameters p and q are independent of current diameter. Most size-related variation in biological fractals can be characterized by allometric scaling laws of the form:

$$Y = Y_a M^b, \qquad (6)$$

where, Y is the dependent variable, M is body mass, b is the power exponent, Y_a is the normalization constant that varies with the nature of Y and with the kind of organism (Enquist et al., 1998; West et al. 1999; Saatchi et al. 2007). The relationship

between Y and M is usually plotted after a logarithmic transformation where;

$$\log Y = \log a + b \log M \tag{7}$$

and if variables Y and M are related, the exponent (b) will indicate their relative proportions over a range of size. If $b = 1$, shapes are geometrically similar or isomeric, (ii) $b > 1$ indicates that scaling is negatively allometric – the form becomes more slender as size increases, and (iii) $b < 1$ suggests that form becomes more robust as size increases.

For fractal models to be applied to shoot or root systems, there are three pre-requisites (Spek and Van Noordwijk 1994; Van Noordwijk et al. 1994; Richardson and zu Dohna 2003):

(1) A test of whether or not the main branch diameter in a branched canopy system can be described with a constant p. A regression of p on the main branch diameter will show whether or not a single value for p can be used and if so which.

(2) For p of approximately 1.0 only the initial branch diameter D_o, the minimum diameter in the system, D_{min}, and the average link length are needed.

(3) Where p is not equal to 1.0, other descriptors, such as q can be used.

Fractal dimension (D_{fract}) is an index of the complexity of the branching system and apparently integrates topological and geometrical parameters (Sugihara and May, 1990; Fitter and Stickland 1992; Berntson 1996; Tucote et al. 1998). The D_{fract} value of an ideally smooth and simple curve is equal to the formal topological dimension ($D_{fract} = 1 = D_{top}$) (Sugihara and May 1990). The complexity of the shape is reflected by the speed with which apparent length changes.

Experiments

Field experiments, designed to study relationships between fractal properties and aboveground C stocks for three tree species in two-year rotation forests, were carried out at Msekera (13º39′S 32º34′E) in eastern Zambia, at an altitude of 1030 m, with a mean annual temperature of 23ºC. The site receives a mean annual rainfall of 1000 mm in a single rainy season and 85% of rain falls within four months (December through March). The soil is an Ustic Rhodustalf, with 26% clay, 61% sand, and 13% silt. Air-dried soil (0−15 cm) had a pH 5.3 (1:2.5 soil/water suspension); KCl extractable Ca, 3.0 $cmol_c\cdot kg^{-1}$ organic C, 10 $g\cdot kg^{-1}$, and total N, 0.7 $g\cdot kg^{-1}$.

Short rotation forests (improved tree fallow) treatments were arranged in randomized complete blocks design (RCBD) with four replicates. The two-year old fallow experiments (2000−2002) comprised stands of *Acacia angustissima* (Mill) (*Acacia*)*, Gliricidia sepium* (Jacq.) (*Gliricidia*)*, Leucaena collinsii* (*Leucaena*). The stands at Msekera were established using potted seedlings in 2000 at a spacing of 1m × 1m in 10 m × 10 m plots. The tree phase was preceded by maize/*Sesbania*-natural fallow- groundnuts-maize rotation.

Destructive sampling of 36 trees, comprising equal numbers of *Acacia, Gliricidia*, and *Leucaena* trees*,* was done in March 2003 for fractal analysis. Measurements of basal diameter (D_{10}), H,

and aboveground biomass were taken according to the procedure described by Kaonga and Bayliss-Smith (2010). Before selecting trees for fractal branching analysis, H and D_{10} measurements of all trees in the central 49 m^2 in each net plot were taken to assess intra-specific variability in the plot. Each randomly selected tree, cut 10 cm above the soil surface, was manually partitioned into four fractions – stem, branches, twigs, and leaves. After weighing individual fractions of each sampled tree on site, samples were bulked according to botanical fractions, over plots in a treatment. Representative sub-samples (500 g) of leaves, branches and stems were then collected from the bulked material and oven-dried at 80ºC for 24 h. However, only 27 trees, representing three species, were processed for fractal analysis of canopy architectures.

Branching characteristics were analysed by examining branching points in entire shoot systems. At each branching point, branches were counted and link lengths between branching points were measured using a tape. Basal and link diameters of all branches before and after the branching points were measured using vernier callipers with a resolution of 0.1 m. Calculations of fresh weight, dry weight and moisture content were based on weights determined before and after oven drying plant samples at 80ºC for 24 h. Since closed canopies affected the accuracy of height measurements, trees were felled and the lengths of the main stems measured using a measuring tape were taken as height values. The tree species had a mean total height of 4.0 m, with a D_{10} of 5.7 cm, and a total dry weight of 6.1 kg.

Figure 1 diagrammatic presentation of functional branching analysis of tree shoot systems in two-year old improved fallows. Beginning from the proximal end of each branch (proximal or initial diameter D_o), the first segment was taken as the first substantial bifurcation and the branches arising from this bifurcation were then classified as internal. The peripheral branches were the most distal links of the branch system consisting of both the terminal branches arising from the branch tips and lateral branches near the periphery. The peripheral links carried leaves over some or all of their lengths. Thus, the number of end structures (I_{end}) and the maximum diameter that still carried end structures ($D_{endstr, max}$) were counted. Diameters of branches were used to calculate parameters p and q for each branching point examined, using Eq. (6) and (7), respectively. Diameter measurements were taken in the middle of a link length. Data collected for each branch consisted of measurements taken on all individual links in a series from the trunk to the terminal branch. The average numbers of branches examined tree^{-1} were 72±36 in *Gliricidia*, 94±46 in *Acacia* and 110±49 in *Leucaena* stands.

Statistical analyses

To test self-similarity across branching orders, scaling coefficients p and q values were regressed on proximal branch diameters. A slope significantly different from zero or a significant change in the parameter distribution with branch size was interpreted as evidence against self-similar branching. Scatter plots were drawn to investigate relationships between different branching variables. Fractal models were developed by regress-

ing log-transformed biomass on fractal variables of the canopy systems using log-linear ($\log y = \beta_0 + \beta_1 \log$) regression procedures of the General Linear Model and 95% confidence intervals, where y is the dependent variable, x the independent variable, β_0, β_1, and β_2 are scaling coefficients. Scatter diagrams were plotted using raw and logarithmically transformed data to visually assess the relationships between aboveground biomass and branching variables.
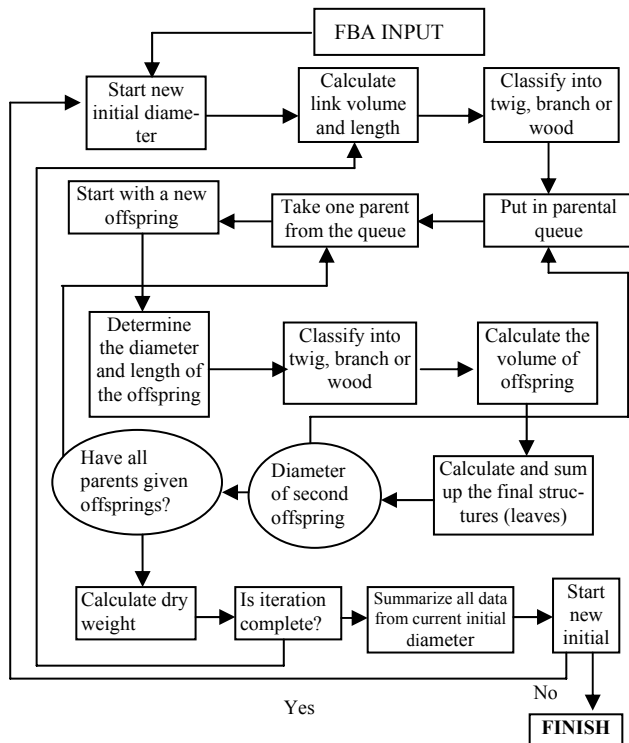
Fig. 1 A model of the functional branching analysis of the tree shoot system (Based on Van Noordwijk and Mulia, 2003).

At each stage, biomass data were statistically analyzed to detect outliers and multicollinearity, test whether an observation strongly influenced the model, and to test the normality of residuals. To homogenize variance over the entire range of sample data, the least square regression technique was applied to log-transformed data and estimates of $\log_{10}\beta_0$ and β_1 were obtained.

Systematic bias introduced by logarithmic transformation of data was corrected using the correction factor of Snowdon (1991). Assessment of the overall fitness of the model was based on the F-value and p-value (Prob > F), coefficient of determination (R^2), average unchanged deviation (% bias), and SEE.

Results

Fractal properties of the canopy architectures

Table 1 shows canopy branching properties of three two-year old short rotation forest tree species at Msekera. The average numbers of branching points with link diameters ≥1.5 cm functionally analyzed were 437 (*Leucaena*), 389 (*Acacia*), and 277 (*Giricidia*). Numbers of branches constituting a branching point in a canopy system ranged from 2 to 5, but 84%–92% of parent branches divided into 2 daughter links. Mean link diameters were similar across species; 3.8±2.0 cm for *Acacia*, 3.8±1.4 for *Gliricidia*, and 3.5±1.2 for *Leucaena*. However, link lengths and numbers of end structures differed between tree species. Link lengths ranged from 62.0 to 81.5 cm, while numbers of end structures declined in the order *Acacia* (51.4), *Gliricidia* (47.7) and *Leucaena* (30.3). Mean D_{fract} values of canopy architectures of *Acacia*, *Gliricidia*, and *Leucaena* were 1.6±0.7, 1.5±0.8, and 1.6±0.2, respectively. However, D_{fract} values ≥1.5 were observed consistently across branching orders with link diameters >1.5 cm.

Basal diameter, total height and total aboveground tree biomass were similar across tree species. Stem biomass of *Acacia*, *Leucaena*, and *Gliricidia* were 2.1, 1.4, and 1.2 kg·tree^{-1}, respectively. Mean aboveground woody biomass of *Acacia* (6.5 kg·tree^{-1}) was substantially higher than those (3.2–3.6 kg·tree^{-1}) of other species. However, total aboveground biomass of *Leucaena* was 8.0 kg·tree^{-1} compared with 6.4 for *Acacia* and 5.0 kg·tree^{-1} for *Gliricidia*, suggesting that fractional allocation of NPP to different plant parts differed with tree species. Woody biomass accounted for 64% to 82% of total aboveground biomass. Basal diameter values for *Acacia, Gliricidia,* and *Leucaena* were 6.2, 6.2, and 4.8 cm, respectively.

Table 1. Branching characteristics of two-year-old *A. angustissima*, *G. sepium*, and *L. collinsii* trees in short rotation forests at Msekera in eastern Zambia

Branching properties	Number of links assessed tree^{-1}	Mean bifurcation ratio (p)	Relative equity among branches (q)	Mean link length (cm)	Average proportion of branching per branching order (%)			Link diameter (cm)
					2	3	>3	
A. angustissima	94.0 ± 46.0	1.7 ± 0.4	0.8 ± 0.2	81.5 ± 55.1	86.1	10.8	3.1	3.8 ± 2.0
G. sepium	72.7 ± 36.5	1.8 ± 0.4	0.8 ± 0.2	70.7 ± 60.4	84.1	12.6	3.2	3.8 ± 1.4
L. collinsii	110.3 ± 49	1.7 ± 0.4	0.8 ± 0.1	62.8± 47.8	91.8	6.6	1.6	3.5 ± 1.2
Branching properties	Average number of end structures	Fractal dimension (D_{fract}) Mean	Link ratio (R_L) Mean	Aboveground biomass (kg·tree^{-1})			Basal diameter (D_{10}) (cm)	Height (H) (m)
				Stem	Wood	Total		
A. angustissima	51.4 ± 49.8	1.7 ± 0.7	1.5 ± 0.3	2.1 ± 1.6	3.6 ± 2.0	6.4 ± 5.6	6.2 ± 1.8	4.0 ± 0.9
G. sepium	47.7 ± 29.6	1.7 ± 0.8	1.7 ± 0.3	1.4 ± 0.5	3.2 ± 1.5	5.0 ± 2.0	6.5 ± 1.5	3.7 ± 0.6
L. collinsii	30.3 ± 27.6	1.5 ± 0.2	1.7 ± 0.3	1.2 ± 0.6	6.5 ± 5.3	8.0 ± 2.4	5.6 ± 1.3	4.0 ± 1.2

R_L, = ratio of mean length of i+1-order branches (L_{i+1}) to the mean length of the i-th order (Li)

Test for similarity across branching orders in the canopies

Fig. 2 shows scatter plots of scaling coefficients p and q against proximal diameters (D_o). The normalization constants for proximal diameter-scaling coefficients plots approached zero. Both p and q were constant across multiple scales of the shoot system at branching orders with diameters $>D_{min}$ (1.5 cm). Mean values of p were 1.7±0.4 for *Acacia*, 1.8±0.4 for *Gliricidia*, and 1.7±0.4 for *Leucaena*, while q was 0.8 for all species. Parameters p and q were branching order independent suggesting self-similarity across multiple scales.
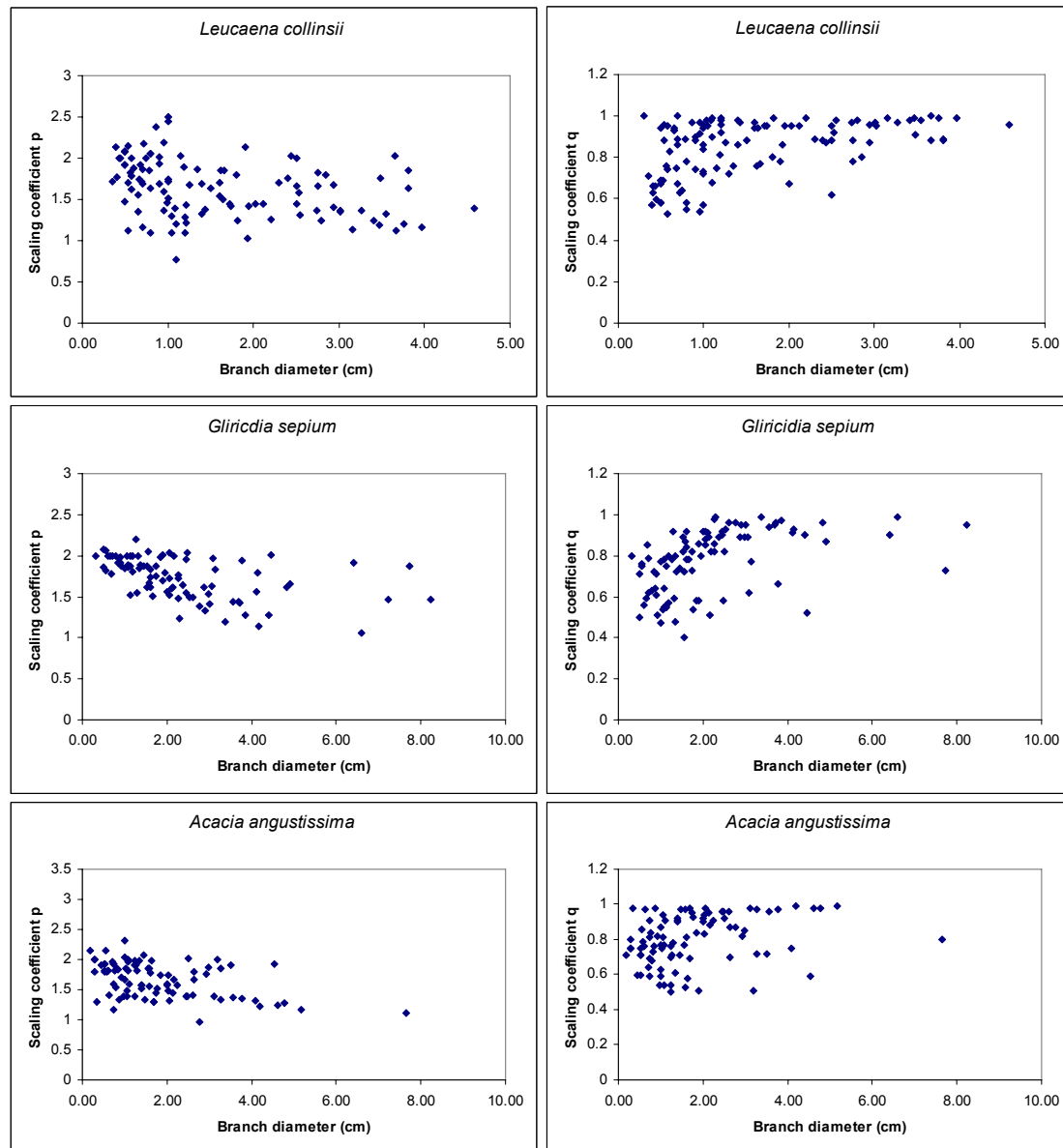

Fig. 2 Scatter plots of proximal (initial) diameter-bifurcation ratio (*p*) and proportionality factor (*q*) against proximal diameter (D$_o$) of canopies in two-year old *Acacia angustissima*, *Gliricidia sepium*, and *Leucaena collinsii* trees at Msekera, eastern Zambia

Relationships between fractal properties of shoot systems

Relationships between link diameters and link lengths in canopy architectures of *Acacia*, *Gliricidia*, and *Leucaena* trees differed across species (Fig 3). Log-linear relationships were observed between link diameter and link length. Link diameter described 57% of variations in link lengths in the shoot systems of *Acacia* and 82% of variations in *Leucaena* trees. Similarly, proximal diameter described 83%−88% of the variability in numbers of leaves on individual trees across species (Fig 4). Proximal diameter (D$_o$)-number of leaves relationships produced positive scaling coefficients (488.2−708.1) and negative normalization constants.
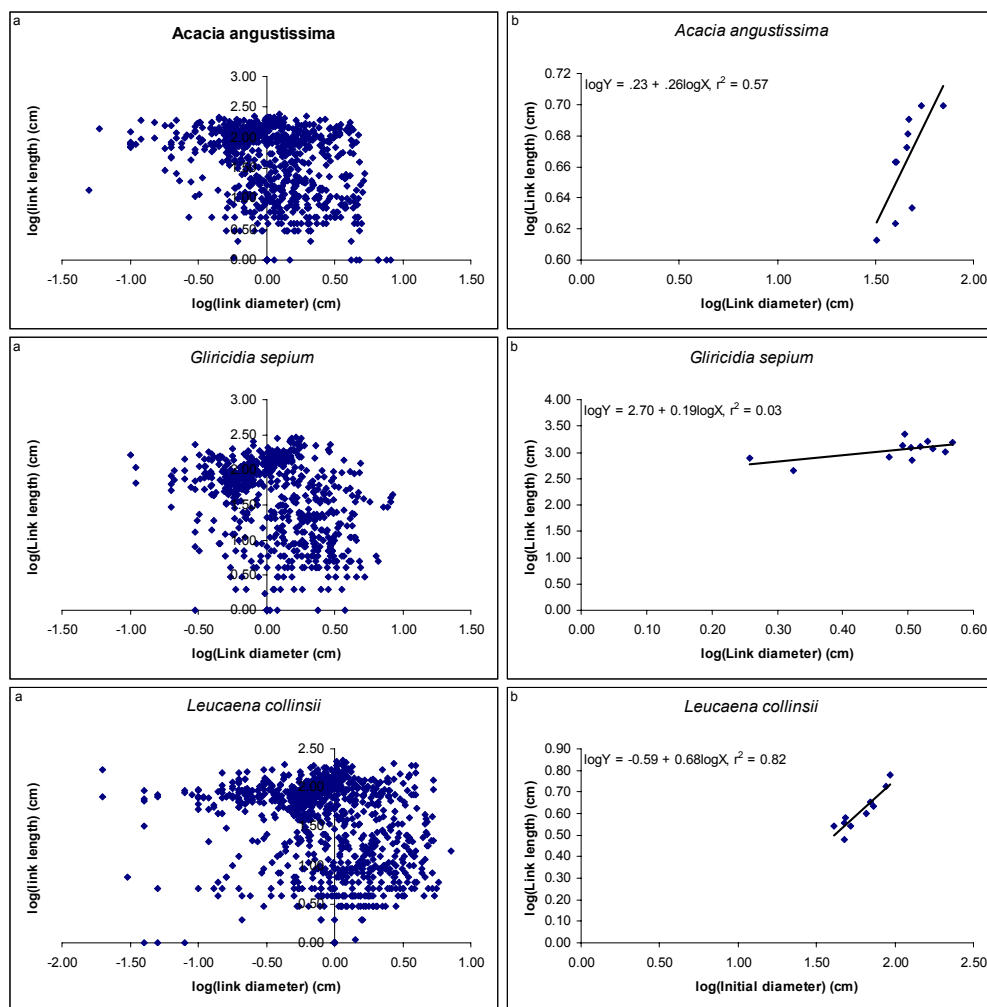
Fig. 3 Log-linear relationships between link diameter and link length in two-year old *Acacia angustissima*, *Gliricidia sepium*, and *Leucaena collinsii* trees at Msekera site, eastern Zambia
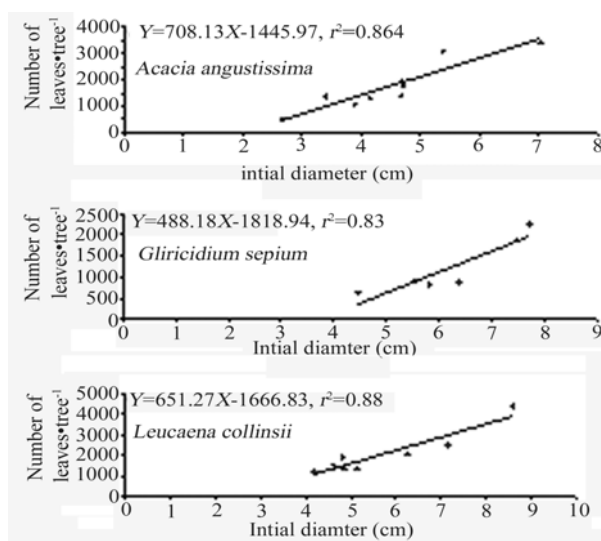
Fig. 4 Log-linear relationships between link diameter and link length in two-year old *Acacia angustissima*, *Gliricidia sepium*, and *Leucaena collinsii* trees at Msekera site, eastern Zambia

The predictor variable, number of branches, described 71-90% of variability in numbers of end structures in shoot systems of the three tree species (Fig 5). The log-linear relationship between the number of branches and number of end structures was stronger in *Leucaena* than in other species. The normalization constants and scaling powers for the functions ranged from -0.12 to -1.41 and from 0.72 to 2.22, respectively. Allometric properties of tree canopies in short rotation forestry systems were strongly related suggesting that regression functions developed using fractal properties could be used to describe selected canopy characteristics.

Fractal models for estimation of aboveground biomass

Log-transformed branch biomass data for *Acacia*, *Gliricidia* and *Leucaena* were linearly related to log-transformed values number of branches (Fig 6). The predictor variable, number of branches, described 79% of variations in branch biomass in *Acacia*, 69% in *Gliricidia*, and 70% in *Leucaena*. The normalization coefficients and scaling coefficients for the number of branches-total branch

biomass log-linear relationships ranged from -1.3 to 0.5 and from   1.8 to 3.0, respectively.
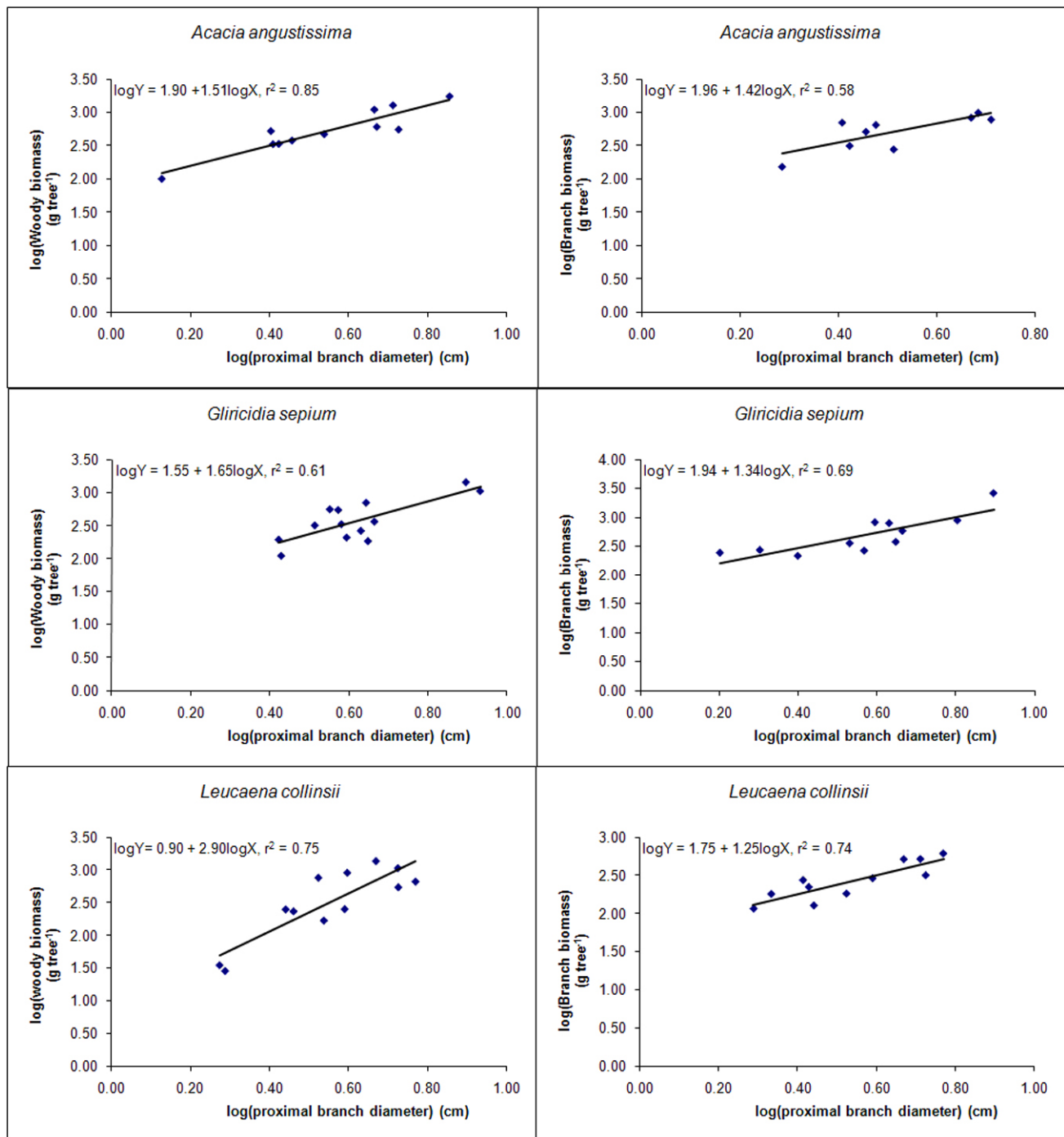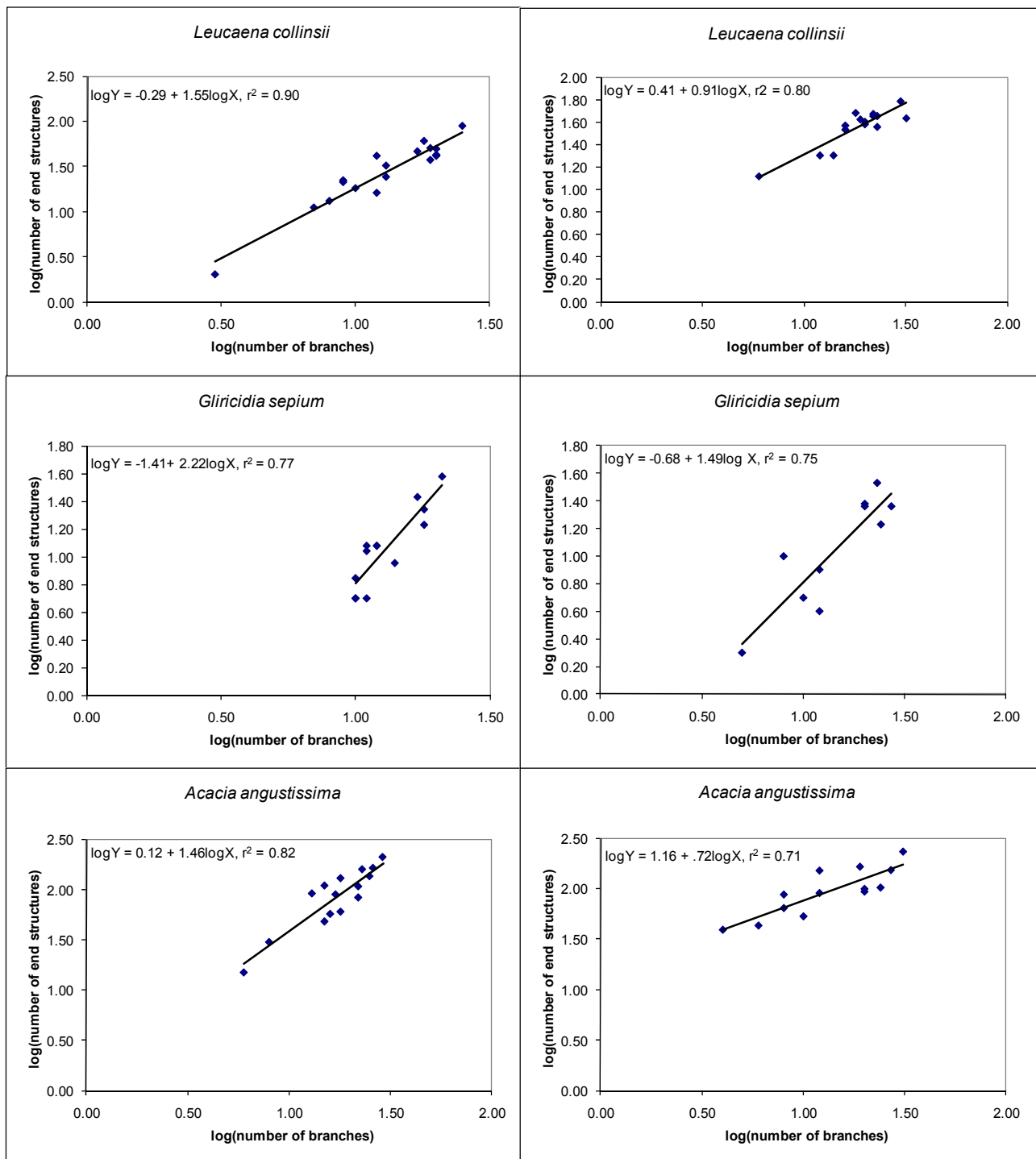

Fig. 5 Log-linear relationships between total number of branches and number of end structures of trees in two-year-old *Acacia angustissima*, *Gliricidia sepium*, and *Leucaena collinsii* trees at Msekera, eastern Zambia

Fig. 7 shows relationships between proximal diameter (D_o) and tree biomass (total woody biomass and total branch biomass) of *Acacia*, *Gliricidia*, and *Leucaena* species. There was a log-linear relationship between proximal diameter D_o and woody biomass with R^2 values ranging from 0.6 (*Gliricidia*) to 0.8 (*Acacia*). The relationship between D_o and total woody biomass

was stronger than that modelled between D_o and branch biomass. The R^2 values for D_o - branch biomass functions ranged from 58 to 74%. The normalization constants and scaling coefficients for the functions ranged from -1.7 to -2.0 and 1.2 to 1.4, respectively. Scatter plots of log-transformed values of D_o against residuals and number of branches against residuals showed that there was

no discernible pattern to the distribution of residuals of regres-   sion.

Fig. 6 Log-linear relationships between number of branches and total dry branch biomass of two-year-old *Acacia angustissima*, *Gliricidia sepium*, and *Leucaena collinsii* trees at Msekera, eastern Zambia

Table 2 shows relationships between D_{fract} and aboveground biomasses (stem, woody, and total biomass) of three tree species. Aboveground biomass data of the three tree species were linearly related to D_{fract} of their shoot structures. D_{fract} accounted for 82-93% of variations in aboveground biomasses of *Acacia*, *Gliri-*

cidia, and of *Leucaena,* with *Acacia*. The biomass functions had positive scaling coefficients (2.4–35.9) and negative normalization constants (-49.7–-2.8). Similarly, proximal diameter accounted for 76%–93% of variability in aboveground tree biomass of *Acacia*, *Gliricidia*, and *Leucaena*.

Basal diameter (D_{10}) described 79%–93% of variations in stem biomass and 78%–94% of variations in total aboveground biomass of assessed tree species (Table 3). Addition of H to regression models in which D_{10} was the main predictor did not significantly improve the goodness of fit. All the models were highly significant ($p < 0.01$) with scaling that was positively allometric.

Table 2. Fractal models for estimation of aboveground biomass (kg tree^{-1}) of two-year-old *Acacia angustissima*, *Gliricidia sepium*, and *Leucaena collinsii* at Msekera site, Zambia ($n = 9$)

Species	Fractal model	R^2	SEE	F value	Sign.
Acacia angustissima	Stem biomass = 10.53 D_{fract} − 14.60	0.93	0.47	117.58	<0.01
	Aboveground woody biomass = 34.40 D_{fract} − 48.11	0.92	1.72	93.4	<0.01
	Total aboveground biomass = 35.87 D_{fract} − 49.75	0.82	2.55	49.8	<0.01
Gliricidia sepium	Stem biomass = 2.36 D_{fract} − 2.80	0.81	0.17	27.19	<0.01
	Aboveground woody biomass = 4.16 D_{fract} − 4.07	0.8	0.33	23.31	<0.01
	Total aboveground biomass = 5.81 D_{fract} − 6.19	0.82	0.39	32.49	<0.01
Leucaena collinsii	Stem biomass = 3.47 D_{fract} − 4.02	0.76	0.3	27.76	<0.01
	Total aboveground biomass = 20.73 D_{fract} − 27.28	0.93	0.66	106.22	<0.01

D_{fract} = Fractal dimension; R^2 = Coefficient of determination; SEE = Standard error of estimate; Sign. = level of significance.

Table 3. Allometric models for estimation of aboveground biomass (kg tree^{-1}) of two-year-old *Acacia angustissima*, *Gliricidia sepium*, *Leucaena collinsii* at Msekera in eastern Zambia ($n = 11$)

Species	Allometric model	R^2	SEE	Sign
Acacia angustissima	Stem biomass = 1.10 D_{10} − 3.21	0.93	0.49	<0.01
	Total aboveground biomass = 3.12 D_{10} − 10.25	0.94	1.47	<0.01
Gliricidia sepium	Stem biomass = 0.35 D_{10} − 0.54	0.81	0.15	<0.01
	Total aboveground biomass = 0.65 D_{10} − 0.19	0.78	0.35	<0.01
Leucaena collinsii	Stem biomass = 0.42 D_{10} − 0.58	0.79	0.29	<0.01
	Total aboveground biomass = 2. 65 D_{10} − 6.89	0.92	0.6	<0.01
Acacia angustissima	Stem biomass = 1.10 D_{10} − 3.21	0.93	0.49	<0.01
	Total aboveground biomass = 3.12 D_{10} − 10.25	0.94	1.47	<0.01
Gliricidia sepium	Stem biomass = 0.35 D_{10} − 0.54	0.81	0.15	<0.01
	Total aboveground biomass = 0.65 D_{10} − 0.19	0.78	0.35	<0.01
Leucaena collinsii	Stem biomass = 0.42 D_{10} − 0.58	0.79	0.29	<0.01
	Total aboveground biomass = 2. 65 D_{10} − 6.89	0.92	0.6	<0.01

D_{10} = Basal diameter; R^2 = Coefficient of determination; SEE = Standard error of estimate; Sign. = level of significance.

Discussion

Functional branching properties of the shoot systems

The numbers of leaves on individual trees were positively correlated ($r = 0.71$) to the number of branching points in all tree species. *Leucaena*, which had the largest number of branching points, also had the largest number of leaves. By contrast, *Gliricidia* had the smallest number of branching points and the least amount of leaf material. The total number of end structures (twigs and leaves) of individual trees, which ranged from 72 (*Gliricidia*) to 110 (*Acacia*), increased with increasing numbers of branching orders. Previous studies (Betram 1989; West et al. 1999; Van Noordwijk and Mulia 2002) also show that species with large numbers of branching points had the largest number of leaves. Most (84-92%) of the branching orders in canopies of the three species bore two daughter branches at each branching point.

However, interspecific variability in branching properties could probably be explained by differences in fundamental physical and biological principles as well as features of architecture, biomechanics, and hydrodynamics of vascular plants, which determine branching pattern in trees (West et al. 1999; Enquist 2002).

Mean D_{fract} values (1.5−1.7) for *Acacia*, *Gliricidia* and *Leucaena* suggested that branching patterns had an increasing magnitude of intricacy. With D_{fract} values ≥1.5, a threshold below which branching systems are considered to be relatively simple (Sugihara and May 1990; Fitter and Stickland 1992; Masi and Maranville 1998), branching patterns within species were approximately stationery – they were self similar with respect to measured parameters. At branching orders with link diameters <D_{min} (1.5 cm), few D_{fract} values were below 1.5 cm presumably because of inaccuracies in parameterization of the algorithm. Bertram (1989) also argues that portions of the plants that are below a certain critical size scale allometrically becoming more slender as size increases, while those above the limit scale near elastic similarity becoming more robust as size increases. How-

ever, branching patterns of the three tree species were predominantly self similar and fractal.
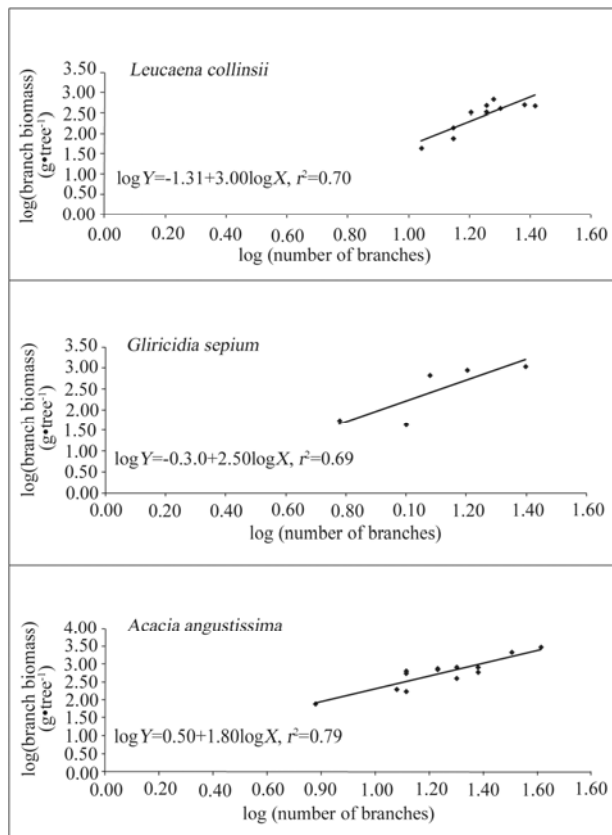
Fig. 7 Log-linear proximal diameter-total woody biomass, and D$_o$ - total branch dry weight, relationships in two-year-old *Acacia angustissima*, *Gliricidia sepium*, and *Leucaena collinsii* fallows at Msekera, eastern Zambia

Test for self-similarity of branching patterns

The normalization constants of the linear regression of scaling coefficients *p* and *q* on branch diameters approached zero and hence the assumption that *p* is independent of scale was valid. The ratio (*p*) was constant across branching orders with link diameters ≥1.5 cm (D$_{min}$). Previous studies have also reported that (1) although some descriptions of tree branch scaling have attempted to use a single uniform relationship governing proportions of trees and branches over their entire range of sizes, portions of plants below a certain critical size scaled differently (Bertram, 1989), (2) the average proportionality factor (*p*) may increase for smaller diameters (Camarero et al. 2003; Richardson and zu Dohna 2003, Allen et al. 2008) because smaller tree branches scale differently from larger branches (Betram 1989), and (3) several models have been parameterized by seemingly rigid morphogenetic rules, but shoot systems have exhibited a high degree of plasticity in their development (Bertram 1989; William 1997; Dzerzon et al. 2003). The D$_o$ of *Acacia*, *Gliricidia*, and *Leucaena,* can be described by a constant *p* across branching orders with link diameter ≥1.5 cm. Since the proportionality factors for total link lengths in canopy architectures of the three

tree species significantly deviated from 1, the assumption of cross-sectional area preservation across the entire shoot system did not hold. Therefore, branch characteristics cannot be predicted with reasonable accuracy from initial shoot diameter unless *p* is used in conjunction with other predictors such as *q*. However, allocation parameter *q* for branching patterns of all tree species was constant at all scales. The proportion of q values >0.9 (f$_q$) was 0.8 for all species.

Relationships between fractal properties

Proximal branch diameter (D$_o$) described most of variations in mean link lengths in shoot structures of *Leucaena* ($R^2 = 0.82$) and *Acacia* ($R^2 = 0.57$) and the relationships were log-linear. Link diameter-link length relationships varied greatly between species presumably because increment in link length per unit increment in diameter (*r*) varied with branch order across species. The parameter with the largest impact on the normalization constant *b* of the allometric equation is *r* or the degree to which link length increases with diameter (van Noordwijk and Mulia, 2002). The relationship between link diameter and link length had a strong bearing on the fractal relationships.

Proximal (initial) diameter described most ($0.83 < R^2 < 0.88$) of the variability in numbers of end structures (twigs and leaves) in *Acacia*, *Gliricidia*, and *Leucaena* canopies. Log-linear relationships between the number of branches and number of end structures were stronger in *Leucaena* than in other species probably because of variability in normalization constants and scaling exponents across species and fractal parameters. Van Noordwijk and Mulia (2002) also observed that slopes differed among properties of the same species. Mean values of D$_{fract}$ were linearly related to those of D$_o$ in canopies of the three species. D$_{fract}$ described 87%–95% of the variations in proximal diameters of *Acacia*, *Gliricidia*, and *Leucaena* with percentage bias of 1.6%–6.6%. Proximal diameter, number of branches, and D$_{fract}$ were strong predictors of canopy branching properties and could be integrated in fractal models for estimation of canopy branching properties.

Fractal models for estimation of aboveground biomass

A log-log linear regression of the number of branches on total dry branch biomass showed that the number of branches accurately predicted branch biomass of *Acacia*, *Gliricidia*, and *Leucaena*. However, variations in branching characteristics at link diameters <D$_{min}$ were evident, presumably because of differences in scaling forms between the small and large branches (Bertram 1989; Spek and Van Noordwijk 1994). However, number of branches described most of the variations in branch biomass representing a significant proportion of total branch biomass. Using a correction factor to account for biomass for link diameters below 1.5 cm, number of branches could be used to predict branch biomass.

Log-linear regression of aboveground woody biomass on proximal diameter (D$_o$) showed that diameter accounted for most of variations ($0.61 < R^2 < 0.85$) in aboveground woody biomass

of *Gliricidia*, *Leucaena*, and *Acacia*. Van Noordwijk and Mulia (2002) also fitted approximately straight lines on a log-log plot of initial diameter against tree biomass and branch biomass. The scaling coefficients (*b*) of diameter-woody biomass and diameter-branch biomass models ranged from 1.2 to 2.9, suggesting that the scaling is negatively allometric (Bertram 1989). Scatter plots of values of D_o against residuals and number of branches against residuals showed that there were no discernible patterns in the distribution of residuals of regression, suggesting that they did not change in a systematic way with allometric variables. The predictive power of D_o was stronger for woody than branch biomass. Thus, D_o is a strong predictor of aboveground woody biomass.

Mean values of aboveground biomass (stem, woody, and total biomass) were log-log linearly related to those of D_{fract} values of the shoot structures, accounting for 82%–93% of variations in aboveground biomasses of *Acacia*, *Gliricidia*, and *Leucaena*. Fractal models had positive scaling coefficients and negative normalization constants. The scaling exponents exceeded 1 (*b* > 1), suggesting that the scaling is negatively allometric (Bertram, 1989). Therefore, D_{fract} is a strong predictor of aboveground biomass of two-year old *Acacia Gliricidia*, and *Leucaena*.

Basal diameter (D_{10}) alone described 78%–94% of the variations in stem, and total aboveground, biomass in two-year old *Acacia Gliricidia*, and *Leucaena* trees. Adding H to the regression model marginally improved the goodness of fit. Previous studies have also showed that H was not a good predictor of aboveground biomass in *Dodonaea viscose* (Litton and Kauffman 2008) and in two-year old *Acacia, Leucaena, Gliricidia, Calliandra callothyrsus,* and *Tephrosia* species (Kaonga and Bayliss-Smith, 2010). Basal diameter was the strongest predictor probably because radial growth as measured by girth proved to be a more reliable parameter than apical growth (Otieno et al. 1991), which is more sensitive to short-term variability in environmental conditions. By contrast, Harrington (1979) and Claesson et al. (2001) argue that allometric equations for estimation of biomass based on only one response variable are of questionable accuracy because trees that have experienced different degrees of competition for light may give erroneous results. Therefore, models with D_{10} and H as predictor variables describe most of the variation in aboveground biomass of short rotation tree species, but D_{10} alone can be used to accurately estimate aboveground biomass and is logistically the most applicable predictor.

Conclusion

This experiment tested a hypothesis that if the shoot systems of *Acacia*, *Gliricidia*, and *Leucaena* were fractals, aboveground tree biomass can be predicted based on fractal properties of the shoot structure. The canopy architectures of the three tree species demonstrated self-similarity at branching orders with link diameter above 1.5 cm, satisfying conditions for application of fractal algorithms for describing branching patterns.

Strong linear and log-log linear relationships were observed between link diameter and link length, number of branches and number of end structures, number of links and number of leaves, and between fractal dimension and basal diameter. Strong relationships among branching properties demonstrated that they could be used to describe the architecture of the canopies of the three species.

Fractal variables (D_{10}, proximal diameter, and D_{fract}, and number of branches) described most of the variations in aboveground biomass (stem, wood, and total biomass) with 95% confidence. Under existing conditions in eastern Zambia, D_{10}, D_{fract} and proximal diameter were strong predictors of variations in aboveground biomass of two-year-old *Acacia*, *Gliricidia*, and *Leucaena*. Thus, the hypothesis that allometric equations for relating aboveground tree biomass to fractal properties could accurately predict aboveground biomass was accepted. However, D_{10} is logistically the most applicable predictor. Since the model is based on short rotation forest trees, this work can serve as a starting point for more detailed models that incorporate different features beyond the scope of this study.

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